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Microbial immobilization of carbon, nitrogen, phosphorus and potassium: implications for forest ecosystem processes[1,2]

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Abstract

Carbon, nitrogen, phosphorus, and potassium immobilization by microbial populations were estimated in 01 litter, 02 litter, and soil (0–10 cm) monthly through one year in a second-growth, mesic hardwood forest, dominated by *Liriodendron tulipifera*. Elemental concentrations of litterfall, roots, and other inputs (dryfall, stemflow and throughfall), of elemental export in groundwater and of litter and soil strata were available from related studies. Elemental concentrations of microbes (bacteria, actinomycetes, fungal mycelia, fungal rhizomorphs, and fungal fruiting bodies) were determined. Using these concentrations and monthly estimates of field microbial populations, elemental pools immobilized in microbes were calculated for the forest floor strata. Highest microbial immobilization of carbon, nitrogen, phosphorus and potassium occurred in 01 litter during May, in 02 litter during July, and in soil (0–10 cm) during September and October. The period of maximum root growth (January–March) coincided with minimal microbial elemental immobilization. Seasonal microbial immobilization patterns suggest (1) advantages to canopy species for winter root growth, and (2) low elemental export by groundwater due to high microbial immobilization during periods of low root uptake.

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Introduction

Forest ecosystems exhibit mechanisms for capture, distribution, and conservation of elements essential to system persistence (Witkamp 1971; Szabo 1974; Dommerques & Mangenot 1971; Gosz *et al.* 1972; Likens *et al.* 1972; Reiners 1968, 1973; Satchell 1974). The mechanisms of nutrient immobilization, mineralization, release, and redistribution (e.g., root uptake) have been postulated to be controlled by belowground decomposer-plant interactions (Parkinson 1967; Witkamp 1971; Henderson & Harris 1974; Harris *et al.* 1975). If we are to investigate interactions of plants and decomposers, procedures are necessary to quantify microbial immobilization and release of mineral elements in forest floor strata through time.

Indirect measurements of microbial immobilization and release of elements have shown microbial influence on element leaching and root uptake (Witkamp 1971; Witkamp & Frank 1969a,b; Witkamp & Frank 1970). Determinations of microbial elemental composition, biomass, and activity are difficult due to rapid metabolic responses to environmental changes, small organism sizes, and inadequate techniques (Parkinson 1970, in prep.; Ausmus & Witkamp 1973; Szabo 1974). In addition, corollary information on inputs (litterfall, root sloughing), exports (CO_2 efflux, soil water percolate), substrates (litter and detrital root pools), and other decomposer organisms (arthropods, nematodes, earthworms) is essential to understanding forest elemental conservation mechanisms (Reichle *et al.* 1975; Mitchell 1974; Frankland 1974; Bell 1974; Jensen 1974; Kaarik 1974; Waid 1974; Lodha 1974).

Our objectives in this paper are to: (1) estimate the microbial immobilization of carbon, nitrogen, phosphorus and potassium monthly in 01 litter (L layer), 02 litter (F and H layers),[1] and mineral soil (0–10 cm); (2) compare microbially immobilized element pools with total element pools in litter and soil strata, (3) contrast microbial immobilization of these four elements with decomposer invertebrate immobilization, and (4) identify possible mechanisms controlling nutrient conservation in a second-growth, mesic hardwood forest.

Materials and methods

The study area is located near Oak Ridge, Tennessee, USA, within a 30 hectare, second-growth mesic hardwood forest dominated by *Liriodendron tulipifera* L. (Edwards & Sollins 1973). Mean canopy height was 30 m; mean stand age was 48 years. Soils within the area are alluvial, cherty silt loams. The climatic regime is humid-mesothermal (Thornthwaite 1948). Mean annual soil temperature is 13°C (Reichle *et al.* 1973b). Soil moisture was rarely limiting, although short periods of drought in the litter layers were detected in late summer (Edwards 1975a).

Litterfall was collected in 25 plastic tubs (0·25 m^2 area) located randomly within the site. Collections were made monthly except during autumnal litterfall when more frequent samples were necessary and during minimal litterfall when sampling frequencies were decreased.

Wong Samplers below the forest canopy were used to collect throughfall (collectors were closed except during precipitation). Troughs around five trees (three tulip poplars, an oak, a dogwood) were used to collect stemflow. Elemental inputs of canopy leaching were calculated by subtracting elemental input to the canopy by precipitation from element input to the forest floor by throughfall and stemflow (Edwards 1975a).

Three tube lysimeters inserted to approximately 60 cm were used to collect soil water. Water was removed biweekly except during periods of high rainfall. Water fluxes used to estimate elemental losses per unit area were estimated using the PROSPER model of water flow through atmosphere-soil-plants (Goldstein & Mankin 1974). We have made the assumption that element export below 60 cm represents losses from the forest since occurrence of feeding roots is infrequent beyond this soil depth.

Elemental concentrations were determined for detrital sources, precipitation, groundwater, and for micro-organisms. Microbial elemental concentrations were determined using forest substrates and microbial populations which were grown in the laboratory; microbial samples were separated from substrates by scraping or flotation (Ausmus & Witkamp 1973). Mean litter elemental pools were calculated from samples taken at two sites within the study area (N.T. Edwards, unpublished data; McBrayer *et al.* 1973). Elemental concentrations were determined monthly at one site (N.T. Edwards, unpublished data) and seasonally (Jan., Feb., Apr., July, Sept., Nov.) at the other (McBrayer *et al.* 1973). Root elemental concentrations were determined monthly (Cox *et al.* in prep.; W.F. Harris and D.E. Todd, unpublished data).

Three elements were detected using a Lira Model 300 gas chromatograph: carbon by flame ionization, phosphorus by flame photometry, and nitrogen by Coulson conductivity (Horton *et al.* 1971, 1973). Analysis of potassium was performed using a Perkin–Elmer Model 403 atomic spectrophotometer.

ATP determinations of samples from 01 litter, 02 litter, and soil (0–10 cm) were the basis for estimating microbially immobilized elemental pools. On eighteen dates during the year samples were extracted using the cold sulphuric acid technique (Lee *et al.* 1971a,b) and analysed for ATP content using the luciferin–luciferase enzyme assay (McElroy 1947) measured with a GeMSAEC centrifugal photometric analyser (Anderson 1969; Coleman *et al.* 1971; Ausmus 1973). Replicate samples were analysed after removal of roots, or roots and invertebrates to provide a correction for non-microbial ATP within each forest floor stratum. Bacterial ATP was estimated as a fraction of each sample based on microbial respiration rates with and without antibiotic amendments determined on a Gilson respirometer (Anderson & Domsch 1973). Using McElroy's (1947) ATP : element content conversion ratios, we established ATP to element conversion ratios for microbial groups grown on litter substrates in the laboratory or scraped from field samples (Table 17.1). The use of the ATP assay to estimate elemental pools of micro-organisms is an extension of the phenomenon noted by McElroy (1947) and many other research workers that although the absolute values of ATP concentration and elemental concentrations change through the microbe life cycle, the ratio of ATP to at least C, N, P, K, Na are quite constant. Therefore, by measuring ATP content of detrital substrates we can accurately estimate microbial elemental pools.

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[1] H layers are inseparable from F or mineral soil due to the minimal litter accumulation at the study site caused by high decomposition rates.

Table 17.1. ATP concentration and carbon, nitrogen, phosphorus, and potassium concentrations of bacteria, actinomycetes, and fungi in logarithmic growth phases and of fungal fruiting bodies and rhizomorphs.

	% dry weight				ATP
Microbial group	C ±2·5*	N ±0·22*	P ±0·05*	K ±0·25*	concentration mg g^{-1} dry wt
Bacteria	50·0	4·00	0·91	1·50	1·0±0·2
Actinomycetes	44·0	4·20	1·00	4·00	2·3±0·1
Fungal mycelia	45·0	2·80	0·24	0·12	2·3±0·1
Fungal fruiting bodies	37·7	4·40	1·00	4·90	2·3±0·6
Fungal rhizomorphs	36·2	4·13	0·93	3·16	2·1±0·7

ATP: element conversions calculated as mg m^{-2} ATP extracted from a stratum (corrected for extraction efficiencies) and separated into bacterial and non-bacterial (all other microbes) using respiration rates with and without antibiotics (Anderson & Domsch 1973). ATP values were multiplied by mean elemental concentrations to estimate mean elemental pool immobilized within microbes of that forest floor stratum.

* Estimates of analytical precision, standard errors of the mean.

Differences in elemental concentrations among life forms of the same microbial population, especially fungi, are real and must be kept in mind when estimating microbially immobilized elemental pools. However, since, at any point in time, the portion of microbial mass which are spores and fruiting bodies is small (Witkamp 1966 estimated 10% of total fungal mass as spores), these concentration differences have been ignored for this first approximation of microbial immobilization.

Results and discussion

FOREST LITTER NUTRIENT STATUS

Examination of differences in patterns of element accumulation in litter among several forest types yield indirect evidence of microbial immobilization of selective nutrients within the upper litter layer. Using estimates of litterfall and litter turnover obtained from decomposition process level studies, estimates of annual deposition and minimal litter nutrient pools were made on the U.S. Forest Service inventory plots within the southern Appalachians. Under high decomposition rates (due to forest litter characteristics and meterological conditions) greater amounts of carbon may be lost annually from O1 litter than litter input. This condition exists in our study area due to favourable substrate quality (low lignin concentration; high nitrogen concentration), litter temperatures rarely below freezing, and rare (late summer) litter moisture deficit (Edwards 1975a). As shown in Fig. 17.1, carbon is accumulated above annual deposition only in pine and pine-hardwood stands. Forests dominated by hardwoods typically retained only the annual carbon input as litterfall. The pattern of accumulation of phosphorus and loss of potassium from litter of several forest types suggested selective immobilization of nutrient elements by litter microbial populations (Fig. 17.1).

The *Liriodendron* forest site shows little nitrogen loss or gain during litter decomposition and retains approximately 82% of the litterfall nitrogen in summer O1 litter (Ausmus & Witkamp 1973; McBrayer *et al.* 1973). This is probably not true of woody litter at the site which has been found to gain nitrogen through time (D.E. Todd, unpublished data). However, nitrogen is preferentially accumulated over carbon (Fig. 17.1). This preferential conservation of nitrogen is even greater in the litter layer of oak stands (Cromack 1972; Kelly 1973) which has a higher initial C/N.

Phosphorus accumulation in litter is affected by forest type (Fig. 17.1). Hardwood stands preferentially accumulate phosphorus over carbon to a greater degree than pine and pine-hardwood stands. The *Liriodendron* stand preferentially accumulates phosphorus above even that of cove hardwood stands.

Potassium seems to be lost from the litter layer equally across forest types (Fig. 17.1). The *Liriodendron* stand retains approximately 38% of the annual potassium input as litterfall compared to approximately 20% in other stands

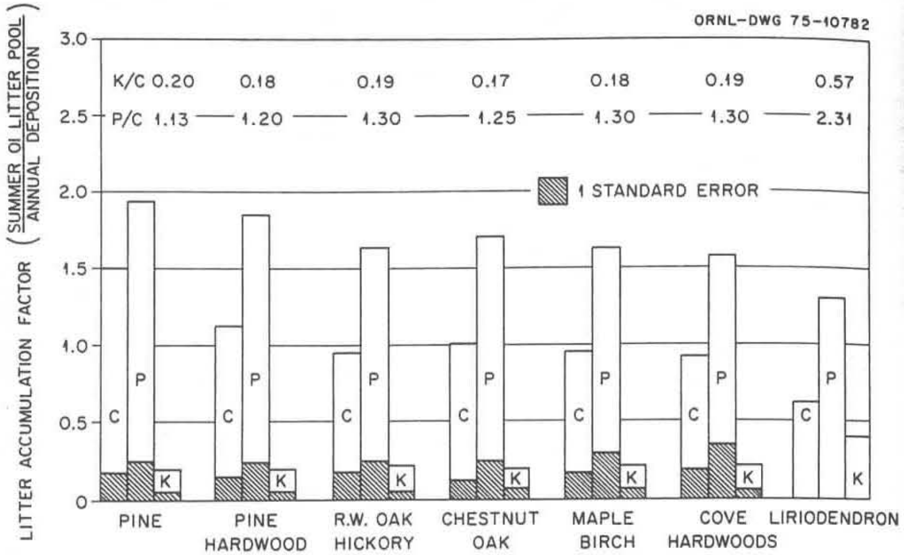

Figure 17.1. Accumulation and loss of elements in the o1 litter layer of forest types occurring within the Appalachian region of the U.S. The litter dynamics of the study site are indicated.

examined. These losses of potassium through the upper litter layer suggest limited control of potassium losses by the litter decomposer community. This hypothesis seems plausible since (1) forest types differ little in litter potassium content, (2) potassium is readily leached, and (3) microbial populations do not concentrate potassium above substrate concentrations (Cromack *et al.* 1975).

Thus, it seems that litter nutrient status is directly dependent upon microbial immobilization of the elements against leaching processes. Elements preferentially immobilized by the microbial community are retained and accumulated in the litter while those not preferentially immobilized are leached. It is necessary to know soil microbial immobilization patterns to determine whether nutrients leached from the litter are lost from the system or available for root uptake.

Microbial immobilization

In o1 litter, maximum microbial immobilization of carbon, nitrogen, phosphorus and potassium occurred during May (Figs 17.2, 17.3, 17.4, 17.5); minimum microbial immobilization occurred during February and March. Carbon immobilization ranged from 1·9 g m^{-2} to 45·2 g m^{-2} (Fig. 17.2) which is equivalent to a maximum of 37% of the o1 litter carbon pool. Nitrogen immobilization ranged from 0·09 g m^{-2} to 3·15 g m^{-2}, equivalent to 2 to 99% of the o1 litter nitrogen pool (Fig. 17.3). Phosphorus immobilization ranged from 0·02 g m^{-2} to 0·58 g m^{-2}, equivalent to 6 to 200% of the o1 litter phosphorus pool (Fig. 17.4). Potassium immobilization ranged from 0·06 g m^{-2} to 1·6 g m^{-2}, equivalent to 11 to 400% if only the o1 litter

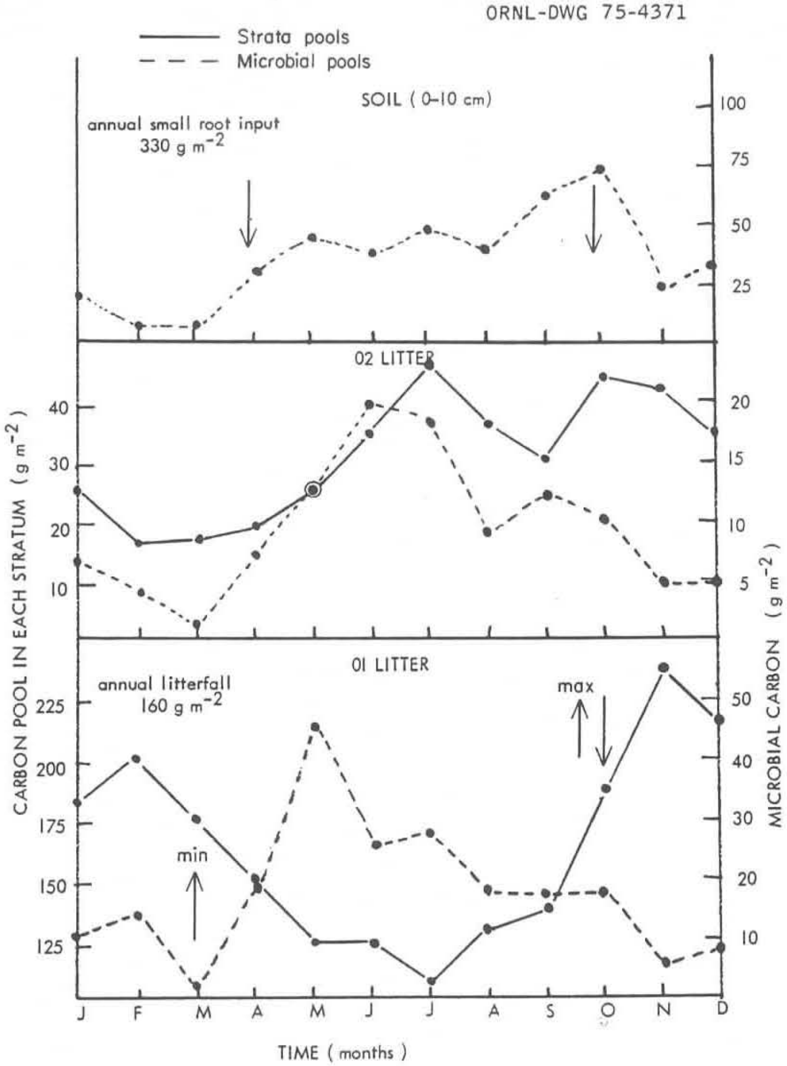

Figure 17.2. Microbial immobilization of carbon in o1 litter, o2 litter, and soil calculated monthly through the year. Carbon pools of o1 and o2 litter are indicated monthly. Periods of maximum litterfall and root sloughing (↓) and maximum and minimum CO$_2$ efflux (↑) are noted.

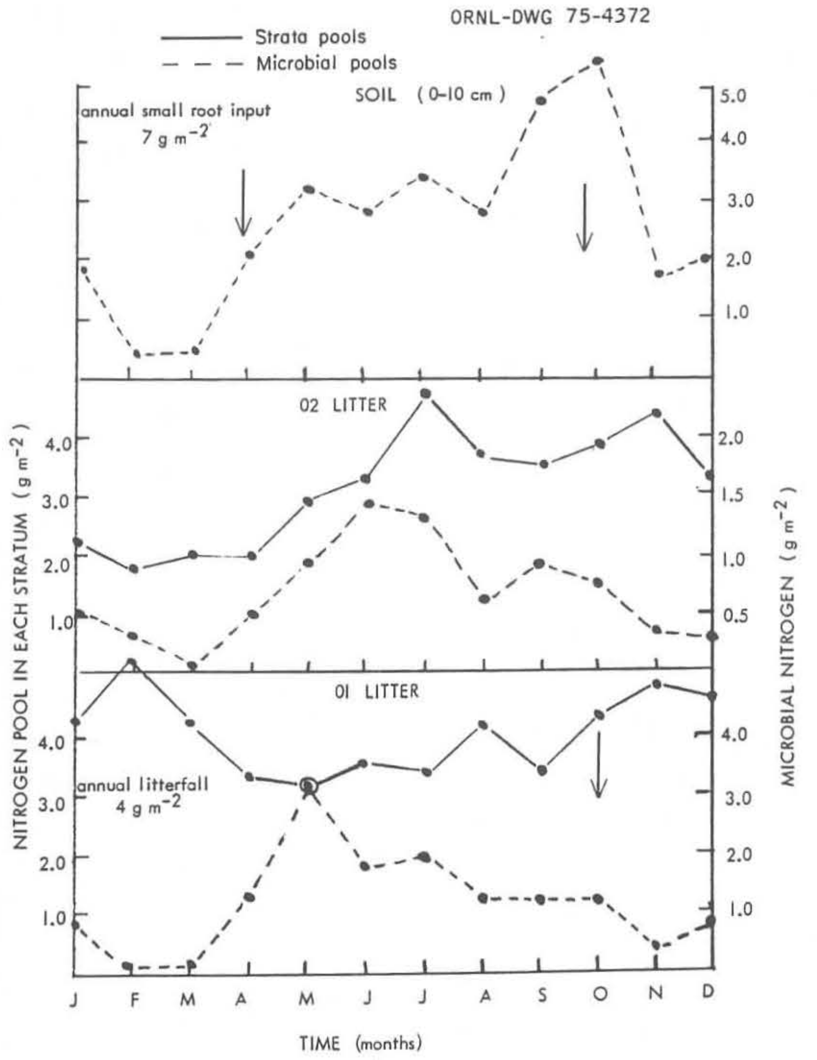

Figure 17.3. Microbial immobilization of nitrogen in o1 litter, o2 litter, and soil calculated monthly through the year. Nitrogen pools of o1 and o2 litter and periods of maximum litterfall and root sloughing are shown with arrows.

potassium pool is considered (Fig. 17.5). It should be remembered that comparison of estimated microbial elemental pools to that of o1 litter layer is simplistic, not considering soluble elemental pools which might be immobilized, nitrogen fixation processes, or translocation of elements from o2 litter and/or soil via fungal mycelial growth and faunal activities. The influence of these processes will be discussed later.

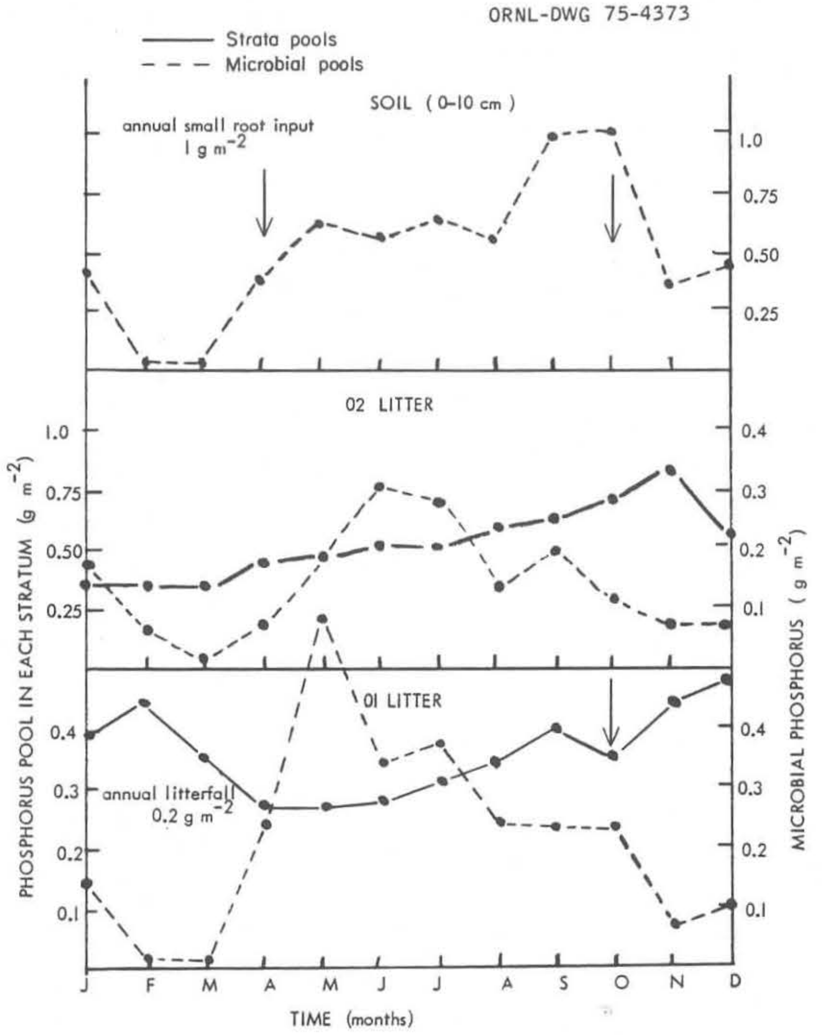

Figure 17.4. Microbial immobilization of phosphorus in o1 litter, o2 litter, and soil calculated monthly through the year. Phosphorus pools of o1 and o2 litter and periods of maximum litterfall and root sloughing are shown with arrows.

In o2 litter, maximum microbial immobilization of the four elements occurred during July, the minimum occurred during March (Figs 17.2, 17.3, 17.4, 17.5). Carbon immobilization ranged from 1·1 g m^{-2} to 19·3 g m^{-2}, equivalent to 3 to 25% of the o2 litter carbon pool (Fig. 17.2). Nitrogen immobilization ranged from 0·08 g m^{-2} to 1·45 g m^{-2} which is equivalent to 4 to 44% of the o2 litter nitrogen pool (Fig. 17.3). Microbial immobilization of phosphorus ranged from 0·01 g m^{-2}, equivalent to 3 to 59% of the o2 litter phosphorus pool (Fig. 17.4). Potassium immobilization ranged

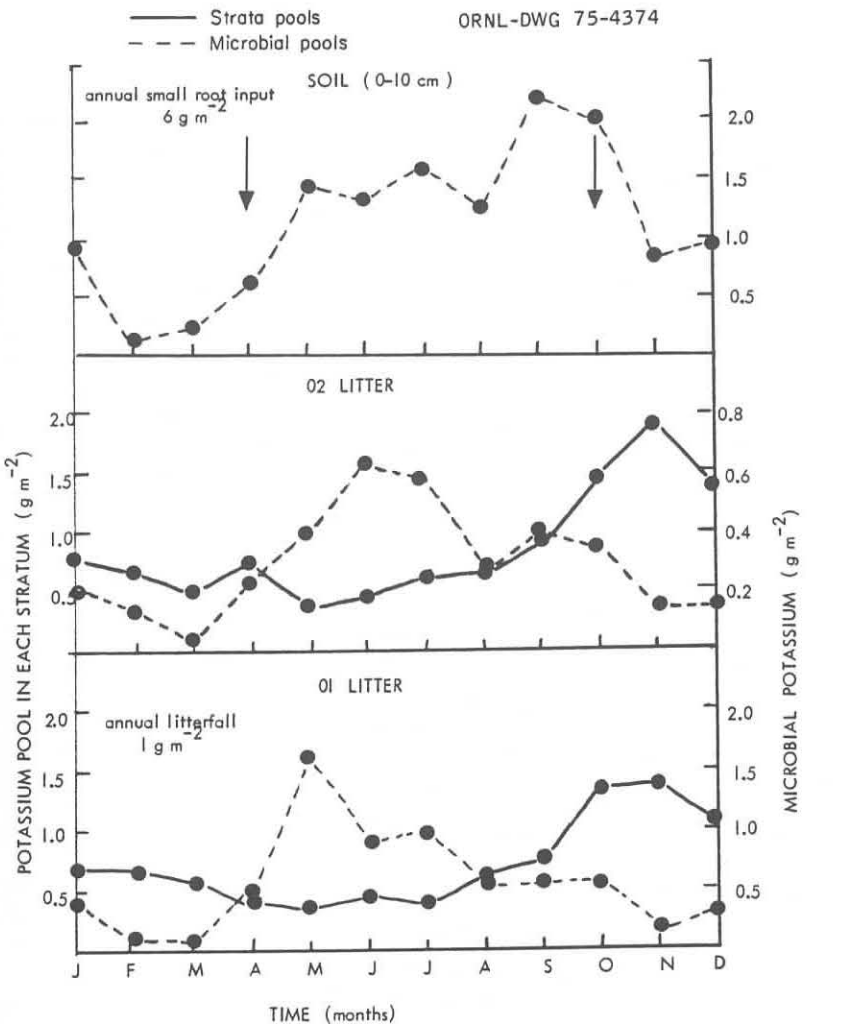

Figure 17.5. Microbial immobilization of potassium in 01 litter, 02 litter, and soil calculated monthly through the year. Potassium pools of 01 and 02 litter and periods of maximum litterfall and root sloughing are shown with arrows.

from 0·04 g m^{-2} to 0·58 g m^{-2}, equivalent to 8 to 91% of the 02 litter potassium pool (Fig. 17.5).

Soil (0–10 cm) microbial dynamics are more stable and immobilize greater amounts of nutrients than either litter layer (Figs 17.2–17.5). Maximum microbial immobilization occurred during September–October with a lesser peak during May. Minimum microbial immobilization in soil, as in the litter layers occurred during February and March. Microbial carbon immobilization ranged from 5·2 g m^{-2} to 73·8 g m^{-2}, much less than the estimated soil organic carbon in these horizons. Nitrogen immobilization ranged from 0·39 g m^{-2} to 5·4 g^{-2}. Phosphorus immobilization ranged from 0·08 g m^{-2} to 1·03 g m^{-2}. Potassium immobilization ranged from 0·18 g m^{-2} to 2·17 g m^{-2}.

Relationship of microbial immobilization to detrital sources and pools

Introduction of carbon, nitrogen, phosphorus and potassium into the detrital food web is dominated by belowground processes. Belowground to aboveground input ratios were 2 : 1 for carbon, 1·5 : 1 for nitrogen, 3·6 : 1 for phosphorus, and 1·4 : 1 for potassium. These estimates include roots <0·5 cm in diameter as the only belowground detrital source, while litterfall, meterological inputs, and canopy leaching were included as aboveground detrital sources (Table 17.2). Aboveground detrital inputs are primarily in the form of litterfall for carbon, nitrogen, and phosphorus (Fig. 17.6). Precipitation inputs were significant for nitrogen, phosphorus, and potassium (8–22%). Canopy leaching accounted for 63% of the potassium input aboveground. Greatest potassium leaching occurred during September and October (Fig. 17.7).

Table 17.2. Detrital and solution sources of carbon, nitrogen, phosphorus and potassium and their export from the *Liriodendron* forest ecosystem.

	g m^{-2} yr^{-1}					
	Detrital Inputs				Exports	
Element	Below-ground small roots	litterfall	Above-ground ppt	canopy leaching	gaseous	ground-water
Carbon	330	160	—	—	1065	1·3
Nitrogen	7	4	0·7	0·2	?	0·35
Phosphorus	1	0·2	0·06	0·02	—	0·004
Potassium	6	1	0·32	2·9	—	0·9

The seasonality of microbial immobilization among the three forest floor strata reflects the periodicity of detrital inputs aboveground and belowground. The rate of increasing immobilization of nutrients in 01 litter in May is greater than that of other forest floor strata caused by increasing spring temperatures (rate of increase approximately twice that of 02 litter and soil). The timing of this burst of microbial activity approximates the period of significant detrital input of *Liriodendron* flower parts and other reproductive structures (McBrayer *et al.* 1973). Summer estimates of micro-

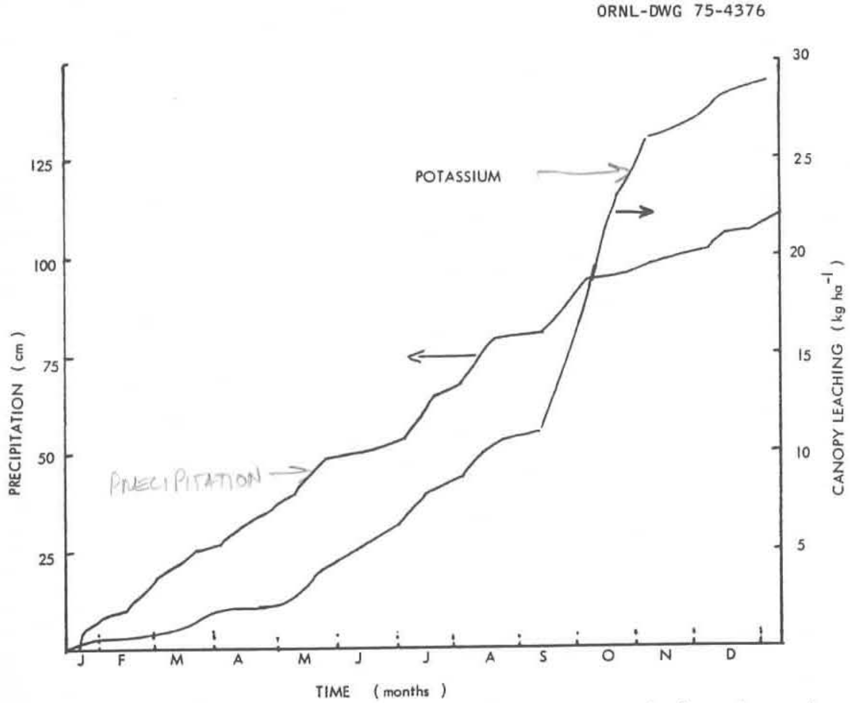

Figure 17.6. Precipitation distribution through the year at the study site and potassium leached from the canopy through time. Notice significant leaching from the last of August into October.

bial immobilization of phosphorus and potassium suggest these elements may be limiting to microbial growth during this period. While translocation of these nutrients from o2 litter and soil and capture of soluble forms of these ions could partially compensate for this implied stress, it is likely that microbial mass is dominated by inactive protoplasm with reduced elemental concentrations (Dowding, this volume, Chapter 7) during this period. A large amount of inactive microbial protoplasm would cause an overestimate of phosphorus and potassium immobilization when based on ATP to elemental conversion factors calculated using data on active growth forms (Cromack *et al.* 1975; Stark 1973).

Microbial immobilization in o2 litter is greatest during the summer. Leaching from the o1 litter layer following short dry periods and the consistently high moisture of soil layers allows high summer microbial activity in the o2 litter layer. Further, there was a high correlation between maximum nutrient elemental pools in o2 litter and maximum microbial immobilization (Figs 17.2, 17.3, 17.4, 17.5).

Soil microbial immobilization peaked twice during the year. Spring increase in microbial activity corresponds to increased soil temperatures,

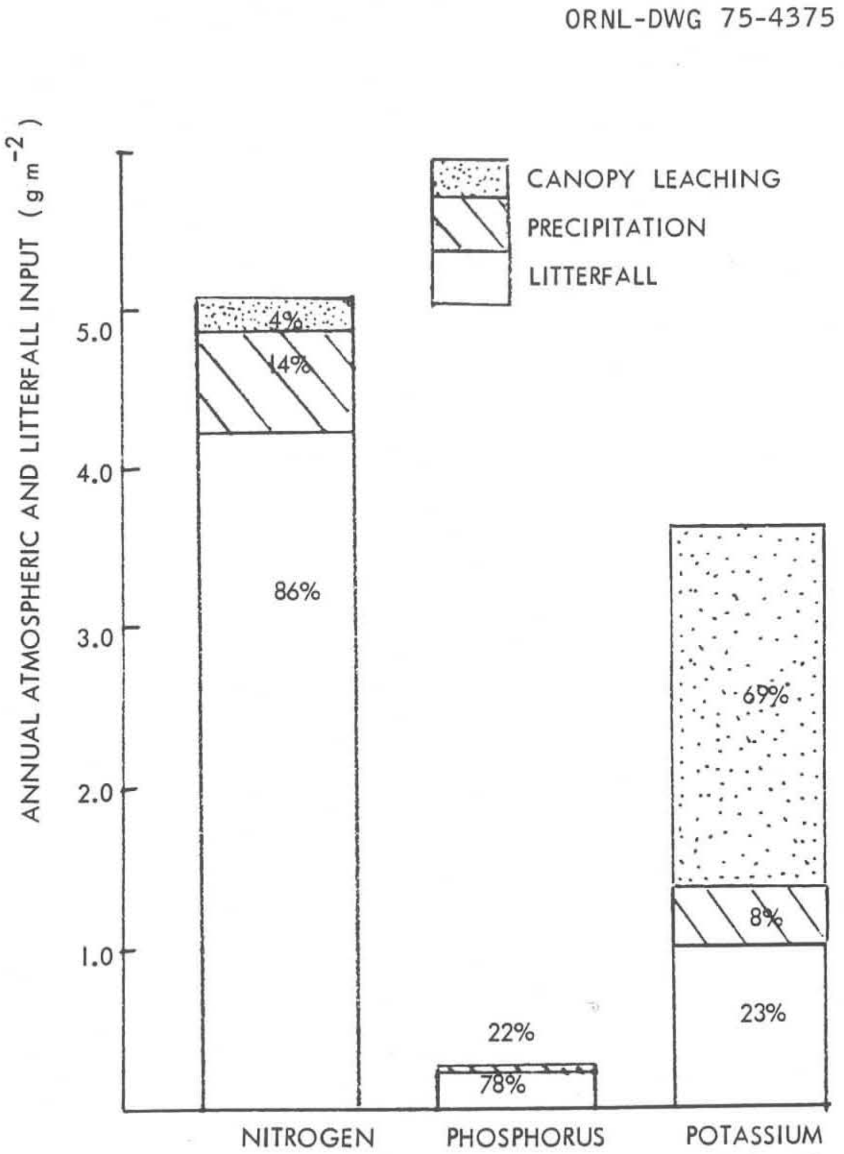

Figure 17.7. Sources of nitrogen, phosphorus, and potassium input to the forest floor from aboveground. Only potassium is significantly leached from the canopy. Significant amounts of the three elements were input as precipitation.

spring *Liriodendron* root sloughing, and input of reproductive parts to the o1 litter layer. Spring microbial activity was expected to be even higher since this is the period of largest root sloughing during the year. It is possible that these sloughed roots are catabolized by the mycorrhizal fungi. If these fungi are at a competitive advantage for these root substrate due to their prior association, their respiration and growth rates would be less than those of fast responding soil microbial species. If the 'sugar microbes' were catabolizing these spring sloughed roots, one would expect to see a period of rapid microbial activity followed by a significant microbial decrease as the populations exhausted the substrates (Fig. 17.2). Summer microbial populations were stable indicating a minimum soil moisture stress during high summer temperatures of the study site. Fall increases in microbial immobilization were correlated with more favourable temperature–moisture regimes, continued catabolism of root detritus, and maximum canopy leaching of potassium. The fall immobilization maximum, greater than the spring peak, may be produced by microbial populations capable of rapid response to changes in solution concentrations of potassium, or other nutrients, within favourable temperature–moisture regimes. The rapid decrease in microbial immobilization by November without drastic temperature reduction supports this hypothesis.

Comparison of microbial and invertebrate elemental immobilization

Using studies of decomposer invertebrates made within the study area, nutrient immobilization by microbial and faunal population were compared (McBrayer *et al.* 1973; Reichle *et al.* 1973, 1975; Ausmus *et al.*, in prep.). Since patterns of immobilization were similar among the four elements examined, nitrogen immobilization will serve as a basis for comparison among decomposer groups (Fig. 17.8).

Arthropod immobilization was weakly correlated to microbial immobilization through the year (McBrayer *et al.* 1973). While arthropod dynamics mimmicked microbial dynamics due to the dominance of the fungus–fungivore trophic pathway, arthropod immobilization averaged sevenfold less than microbial immobilization of nitrogen (McBrayer *et al.* 1973). Arthropods averaged higher nitrogen immobilization than other faunal groups, but during winter earthworms immobilized as much nitrogen as arthropods. Nematode immobilization of nitrogen was an order of magnitude less than that of earthworms and arthropods (Fig. 17.8).

During February and March, arthropods and earthworms immobilize as much as nitrogen as microbial populations which are at an annual minimum. Significant amounts of nitrogen, or other elements were not leached out of the decomposition strata into groundwater. We believe this to be the result of significant root uptake activity during this period. Nematodes, dominated by phytophages, probably have little effect on nutrient dynamics directly by immobilization, but may greatly affect nutrient dynamics increasing decomposer community by forming the lowest link in the soil decomposer food web and by affecting live root processes (mycorrhizal induction and root harvest).

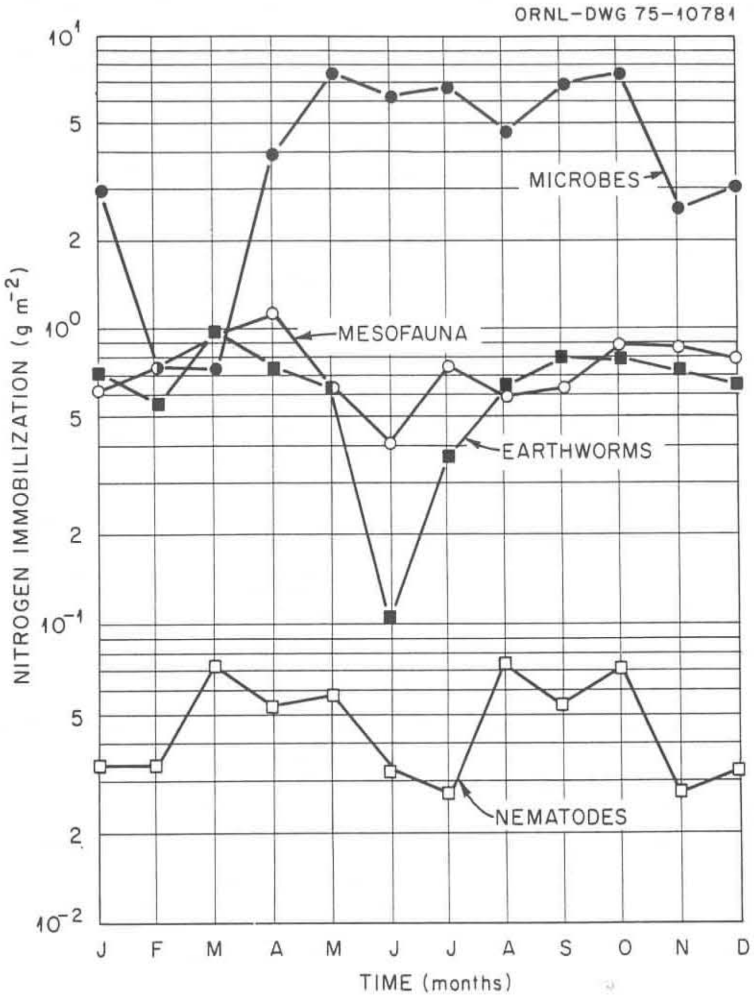

Figure 17.8. Comparison of microbial nitrogen immobilization with that of mesofaunal arthropods, earthworms, and nematodes. While microbial immobilization is much greater than that of faunal, faunal immobilization is much more constant through the year.

Implications of microbial immobilization patterns to ecosystem processes

Within this *Liriodendron* forest the gross primary production was 2,162 g carbon m^{-2} yr^{-1}. Autotrophic respiration (including the entire root community), was 66% of the gross primary production (1,436 g cm^{-2} yr^{-1}). Of the net primary production, 42% was expended for decomposer respiration (670 g cm^{-2} yr^{-1}) leaving a net ecosystem production of 56 g cm^{-2} yr^{-1}. The forest floor (litter and soil) of this forest annually has a CO_2 efflux of 1,065 g cm^{-2} yr^{-1} of which 20–35% evolves from root activity (20% if rhizosphere microbial respiration is separated from root respiration, Reichle *et al.* 1975). The currency for translocation and retention of nutrient elements is carbon allocated for maintenance of the primary producers and decomposers. Over long time periods carbon is accumulated, primarily as soil organic matter, which serves as the biochemical framework for element immobilization by decomposers and redistribution to primary producers via root uptake. While the biochemical form of carbon (e.g., sucrose vs cellulose) limits the rate of microbial and faunal catabolism, the total availability of carbon is not limiting to decomposers during any period of the year.

Nitrogen is preferentially accumulated over carbon in all forest floor strata. Availability of nitrogen is extremely limited in 01 litter foliage and especially woody substrates. While calculations of microbial immobilization of nitrogen suggest almost all 01 litter nitrogen could be within microbial cells during May, translocation of nitrogen from 02 litter and from soil and nitrogen fixation processes in woody litter (Ausmus, unpublished data from *Liriodendron* site and J. Roskoowski, unpublished data, Hubbard Brook) could supplement nitrogen availability. It may be hypothesized that translocation of nitrogen and nitrogen fixation rates in substrates are controlled by substrate nitrogen concentrations.

Minimal decomposer nitrogen immobilization occurs at the season (February–March) of maximum root growth in the *Liriodendron* stand (Harris *et al.*, in prep.). This is also the season that nitrate and ammonia are readily available from soil solution for root uptake due to near saturated soil conditions (G.H. Henderson, unpublished data). Even though considerable soil water percolation occurs during this period (February–March) less than 3% of the annual detrital nitrogen input is lost to groundwater. The phase shift between high microbial immobilization and maximum assimilation of nitrogen in new root tissue is strong evidence that the interaction of autotroph and decomposer populations within this forest ecosystem represents a system-level mechanism for effective nitrogen retention, controlled remineralization and redistribution to support sustained autotroph productivity.

Phosphorus is preferentially accumulated over carbon in 01 litter. This element is probably limiting to litter microbial populations from March through July. We have no direct evidence that this limitation is met by translocation from 02 litter and soil or by decreased microbial phosphorus concentrations.

By contrast, potassium inputs are dominantly soluble, and not retained in 01 litter. While this forest retains 38% of the annual potassium input in 01 litter, other forest types retain an average of 20%. This suggests limited biological control of potassium movement in litter. Further, potassium is limiting to 01 litter populations from April through July (immobilization estimates>available pool). However, groundwater losses of potassium are less than 10% of the annual detrital input. Therefore, it would seem that control of potassium loss is retained in soil but not litter. Well-known soil chemical reactions involving ionic equilibria of soil solution and the organic–inorganic exchange complex could account for conservation of potassium in the soil.

The strategy of elemental retention and redistribution within the forest system, we hypothesize, is dependent upon maintenance of the forest floor (litter and soil) detrital pools and its decomposer community. The cost to the forest is primarily carbon lost in heterotrophic respiration. Seasonality of microbial immobilization of carbon, nitrogen, phosphorus, and potassium within forest floor strata with maximum immobilization occurring at different times among strata and minimum immobilization synchronized with likely periods of maximum root uptake resulted in low amounts of nutrient export from the forest. Decomposer invertebrates, while possessing smaller immobilized pools of these elements may regulate microbial immobilization and release rates through harvest (Mitchell 1974) or indirectly via substrate influences (Van der Drift & Witkamp 1960; Witkamp & Crossley 1966; Patten & Witkamp 1967; McBrayer 1973). Maximum growth of *Liriodendron* roots (defined to include the accompanying root community of mycorrhizal fungi and root surface microbes) occurs at the time of minimum decomposer nutrient immobilization. This harmony between plants and decomposers, we believe, is the major mechanism underlying forest nutrient conservation to support sustained productivity.

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